NEW ANATOMICAL CHARACTERS IN FOSSIL CORALLINE ALGAE AND THEIR TAXONOMIC IMPLICATIONS

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ABSTRACT. Interfilamental cell-connections are considered important characters in the suprageneric and generic taxonomy of present-day nongeniculate coralline algae but to date they have not been used in the taxonomy of fossil corallines. SEM observations of polished and etched specimens allow recognition of interfilamental cell connections in fossils and therefore these characters can also be applied to the taxonomy of ancient coralline algae. The shape and number of epithallial cells, which are important diagnostic features in delimiting genera in the subfamily Melobesioideae, can also be recognized. The implications of this work are that many fossil corallines have to be reassigned to different genera and can also be assigned to the subfamily classification used for present-day corallines. An identification key is given, which permits identification of the known fossil Cenozoic coralline algae using similar criteria to those used for modern corallines.

TRADITIONALLY, generic and suprageneric taxonomy of present-day nongeniculate corallines was based on the characteristics of tissues and reproductive structures, which could be easily recognized in fossil material with normal microscope procedures. As summarized by Wray (1977), diagnostic supraspecific criteria for present-day and fossil material included: (a) type and location of conceptacles; (b) character of hypothallium; (c) character of perithallium, and (d) presence or absence and arrangement of heterocysts (trichocytes).

More recently, Johansen (1969) discovered that interfilamental cell-connections (Text-fig. 1A–B) may be used as important characters to delimit coralline algal subfamilies. Since, Cabioch (1971, 1972), Adey and Johansen (1972), Johansen (1976, 1981) and Woelkerling (1987, 1988), employed the type of cell-connections in both the suprageneric (Table 1), and generic taxonomy of corallines, and this point of view seems now to be widely accepted by botanists working with modern corallines.

In addition to the above characters, Adey (1970) employed the shape of epithallial cells as diagnostic features in delimiting some genera. The number of epithallial cells was also considered by Johansen (1976) to be of diagnostic significance at the generic level and even the pattern of cell elongation was used in distinguishing supraspecific taxa (Adey 1964; Adey and Johansen 1972; Woelkerling and Irvine 1986). Other anatomical features hardly observable or preservable in fossil specimens, such as the emplacement of conceptacle primordia (Adey 1964; Adey and Johansen 1972), the pattern of spore germination (Chamberlain 1983), the presence of haustoria (Woelkerling 1988) and the presence of plugs in conceptacle pores (Woelkerling 1987, 1988), have also been introduced as diagnostic criteria in generic and suprageneric coralline taxonomy.

Many of these characters have not been recognized in fossil material and therefore the taxonomy of present-day corallines has become separate from the taxonomy of fossil corallines. These differences between the palaeontological and neontological classifications led Wray (1977, p. 58) to assume the impossibility of using these new criteria in dealing with fossil algae and led Poignant (1984, p. 603) to conclude that the generic taxonomy of fossil corallines must be independent of that of modern algae.

The aim of this paper is to show that key features such as cell-connections are commonly preserved and can be recognized in fossil corallines. Epithallial cells and meristems are also

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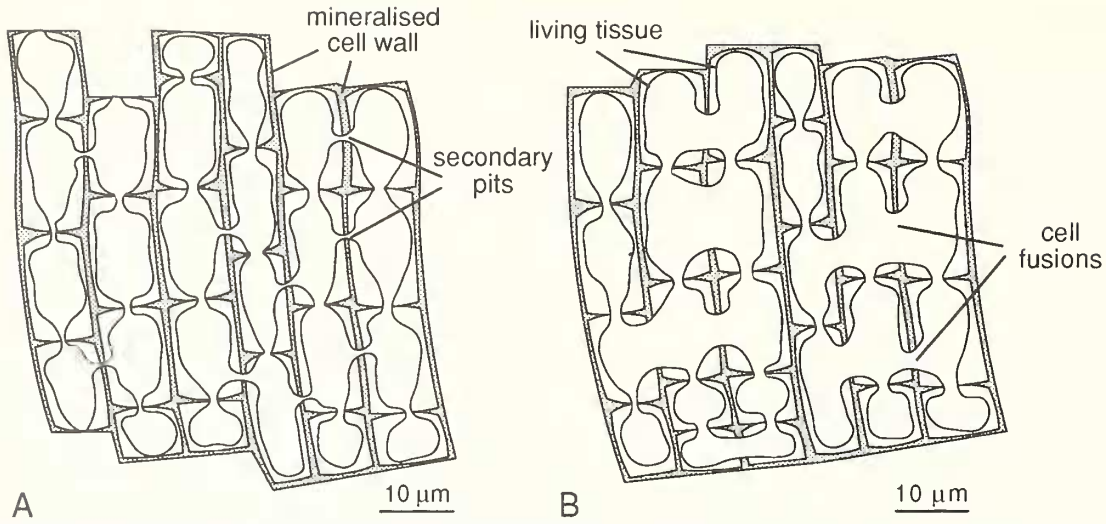


TEXT-FIG. 1. Scheme of the two types of interfilamental cell connections. A, secondary pit connections. B, cell fusions.

TABLE 1. Subfamily classification of the nongeniculate coralline algae (from Johansen 1981, Woelkerling 1987, 1988).

Subfamily	Cell fusions joining contiguous filaments	Secondary pit connections joining contiguous cells	Sporangial conceptacles; tetraspores
Lithophylloideae	No	Yes	Uniporate; tetraspores lacking plugs
Melobesioideae	Yes	No	Uniporate; tetraspores lacking plugs
Mastophoroideae	Yes	No	Multiporate; tetraspores with plugs
Choreonematoideae	No	No	Uniporate; tetraspores with plugs

sometimes calcified and can occasionally be observed in fossil material. Using appropriate SEM techniques we show that it is possible to use the same taxonomic criteria, whether the material is fresh, dried or fossilized, and that fossil material can be identified at generic and subfamily level using the taxonomic systems currently used by botanists (Table 1; Woelkerling 1988). It is crucial for understanding the history of the group and to developing the potential of these algae for palaeoenvironmental interpretations that the taxonomy of fossil and present-day corallines is as close as possible.

METHODS

Thin sections

Fossil corallines are commonly studied in thin sections using petrographic optical microscopes. It is important to emphasize that the algal thalli must be properly orientated in order to visualize the tissue organization and the conceptacle morphology. Usually two types of sections are needed for

this purpose: one parallel to the direction of filament growth and perpendicular to the thallus surface, and the other perpendicular to the direction of filament growth for measurement of cell diameters. Observations made in sections with other orientations may help in recognizing anatomical features but data obtained exclusively in sections other than the two basic orientations can be misleading. There are many examples in the literature of incorrect interpretations of tissue organization of fossil coralline species, which are based on inadequate or insufficient sections. Thin sections should be thinly ground and ideally should be not much thicker than the cells are wide (usually less than 20 μm). Thick sections preserve a number of superimposed filaments and cells which are difficult to interpret.

SEM techniques

The procedure which we have found to produce the best results is to prepare samples of fossil corallines for scanning electron microscopy following the steps below.

(a) Thalli are split with the aid of a small chisel or wire cutters into 5 to 10 mm pieces which are the most convenient size for handling.

(b) These pieces are oriented and embedded in a resin and the surface is cut and polished. Two sections should be made; one parallel to, and the other perpendicular to the direction of filament growth. The specimen is oriented best with a dissecting microscope.

(c) The polished surface is etched with EDTA (7% vol.) or HCl (2% vol.). The appropriate etching time largely depends on the diagenesis of the sample but, for most specimens, 3 minutes using EDTA and one minute using HCl yields good results. Cell size in the coralline thallus also influences the appropriate etching times.

(d) The samples must then be mounted on stubs and coated with carbon and/or gold following standard scanning microscopy procedures.

The procedure used in preparing modern corallines, by simple fracturing of thalli prior to mounting and coating of the sample, does not give good results in fossil material as diagenetic features obscure the original tissue characteristics. After the polishing and etching of fossil coralline thalli, however, original cell walls and successive cements are clearly distinguishable (Pl. 1, figs 1–2) and the structure of calcified tissues is observable at magnifications similar to that used by botanists. We have found that sometimes cell walls etch positively and sometimes negatively with respect to the cements infilling the cell cavity. This occurs in material from the same horizon which has been etched in the same way. We have no explanation as to why this should occur, but would expect the smaller-celled micritic walls (with larger surface areas) to react faster to etching and preferentially to dissolve out.

RESULTS

Cell connections

The types of interfilamental cell-connections are considered a diagnostic feature in delimiting subfamilies, and hence genera, of present-day corallines. With the SEM or optical thin-section procedure described above, interfilamental cell fusions are easily recognizable in fossil corallines (Pl. 1, figs 1–2; Bosence, in press) and therefore we are able to use this character for the first time in taxonomy. Cell fusions can be seen as voids extending from a cell of one filament to a cell or cells of contiguous filaments. Cement(s) lining these voids delineate the original shape of fused cells and clearly distinguish these original tissue features from fractures or later recrystallization of coralline skeletons. In addition, diagenetic recrystallization of cell walls occurs in patches and not in discrete, lateral intercell connections. Secondary pit-connections, although observable in some cases (Pl. 1, fig. 3), are more difficult to recognize as they are too small to allow cements to penetrate and fill them. When cell fusions are absent, and the interfilamental cell-connections are secondary pits, filaments appear as continuous and aligned rows of cells which are clearly delimited from adjacent ones by continuous cell walls (Pl. 1, fig. 4).

When the sample preparation for SEM work described above is applied to present-day coralline

thalli, the results are similar to those obtained in fossil corallines. Cell fusions are infilled by impregnating resin or by cements in the older parts of the thallus. The response of these infillings to etching is different from that of the calcified cell walls and the different final relief shows the structure of tissues (Pl. 1, fig. 5). Secondary pit-connections usually remain as empty, small holes in the cell walls and are only visible occasionally as cement moulds. When cell fusions are absent however, filaments are continuous and aligned, and clearly delimited from contiguous ones (Pl. 1, fig. 6).

In thin section the interfilamental cell-connection type is also recognizable, although it is initially less clear and unequivocal. Coralline tissues with interfilamental cell fusions have a spongy appearance in thin section, i.e. they are made up of irregularly sized and shaped cells, and cell fusions are visible as discontinuities in lateral cell walls (Pl. 2, fig. 1). Fracturing and recrystallization of tissues, however, may be misleading and hardly distinguishable from original features of tissue at the low magnifications usual in optical microscopy. When cell fusions are absent the tissue in thin section shows clear and continuous filaments which give a tissue a characteristic structure (Pl. 2, fig. 2).

As an example of the taxonomic implications of these microstructural studies in fossil corallines we have re-examined two late Miocene coralline species from southern Spain and Malta (see Systematic Palaeontology section below). The evidence obtained from SEM analysis substantially changes the subfamilial and generic ascription which would have been previously applied to these species following traditional palaeontological taxonomy. In both examples, SEM analysis clearly shows the presence of cell fusions (Pl. 1, figs 1–2). These may also be seen in thin sections (Pl. 2, figs 1, 3) and can be confirmed by SEM. Together with the tetra–bisporangial uniporate conceptacles and non-geniculate thallus, these morphological characters undoubtedly place these species in the subfamily Mastophoroideae (Table 1; Woelkerling 1988).

These examples indicate major changes in the taxonomic status of some, or even many, fossil Cenozoic coralline species. The recognition of cell fusions will require species with uniporate tetra/bisporangial conceptacles, and considered in the past to be members of the subfamily Lithophylloideae, to be transferred to the subfamily Mastophoroideae. In our experience, many fossils previously ascribed to *Lithophyllum* in the Mediterranean Tertiary are probably either *Spongites* or *Neogoniolithon*. There are no previous references to Tertiary *Spongites* apart from our preliminary work on this project (Bosence in press; Braga *et al.* 1990; Braga *et al.* 1991), as *Spongites* has been a long-overlooked genus until its reassessment by Woelkerling (1985). Segonzac (1972, 1990) referred several coralline species from the Neogene of eastern Spain to *Neogoniolithon*

EXPLANATION OF PLATE 1

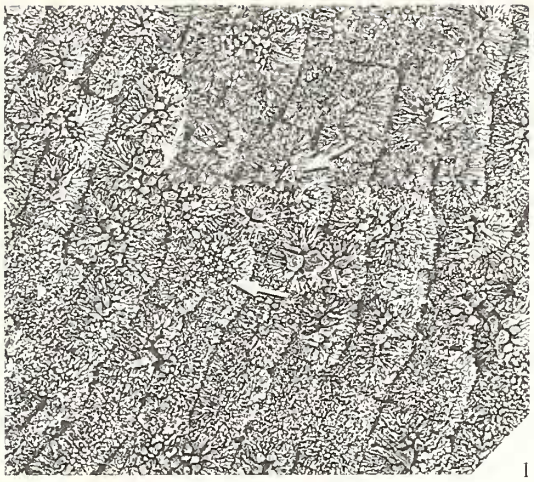
Figs 1–2. *Spongites* sp. 1. Museo de Paleontología Universidad de Granada, Sample TJ-21; Almanzora Corridor, Almería, Spain; upper Tortonian. 1, longitudinal section of perithallial filaments showing lateral cell fusions (arrows) preserved by infilling cement; direction of growth towards top of figure, × 450. 2, detail of Fig. 1 showing lateral cell fusions (arrows), × 900.

Fig. 3. *Lithophyllum* sp. BMNH, V.63740; secondary pit connection (arrow) between adjacent perithallial cells; cell walls have been etched by HCl; Malta; upper Tortonian, Upper Coralline Limestone Formation (location 39 of Bosence 1983), × 2000.

Fig. 4. *Lithophyllum* sp. Museo de Paleontología Universidad de Granada, Sample TJ-25; longitudinal section showing continuous cell and filament walls; direction of growth towards top right; Almanzora Corridor, Almería, Spain; upper Tortonian, × 500.

Fig. 5. *Spongites* sp. Museo de Paleontología Universidad de Granada, Sample PR-8; Recent specimen in longitudinal section with resin infill to cell cavities and etched cell walls showing lateral cell fusions; La Caleta, Cádiz, Spain, × 500.

Fig. 6. *Lithophyllum* sp. Museo de Paleontología Universidad de Granada, Sample PR-10; longitudinal view of Recent specimen showing filaments with continuous filament walls and secondary pit connections (arrows); La Caleta, Cádiz, Spain, × 500.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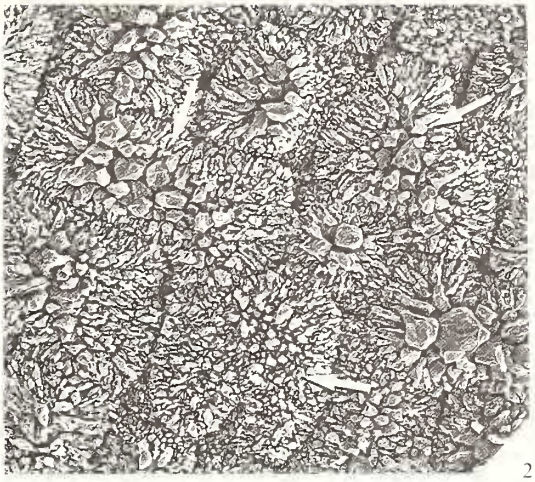
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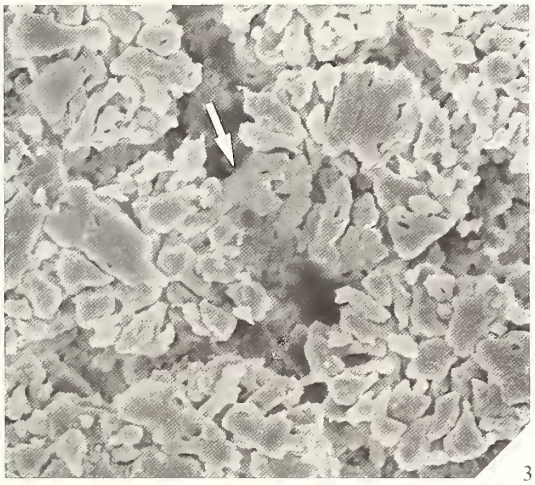
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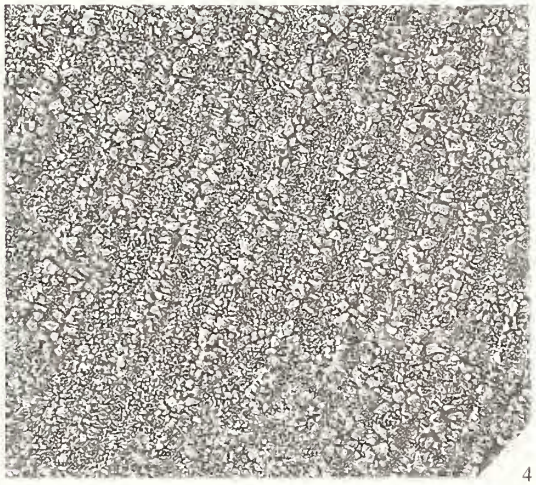
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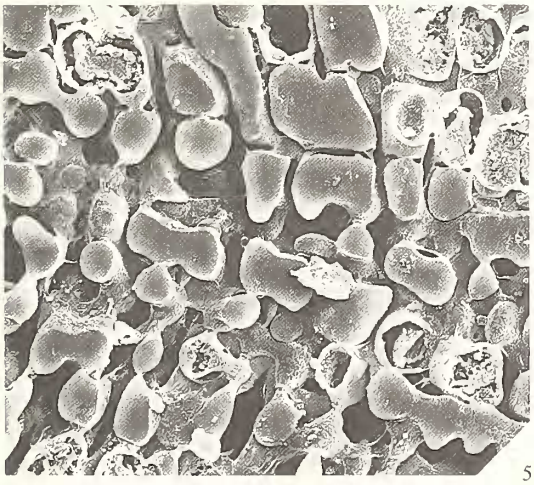
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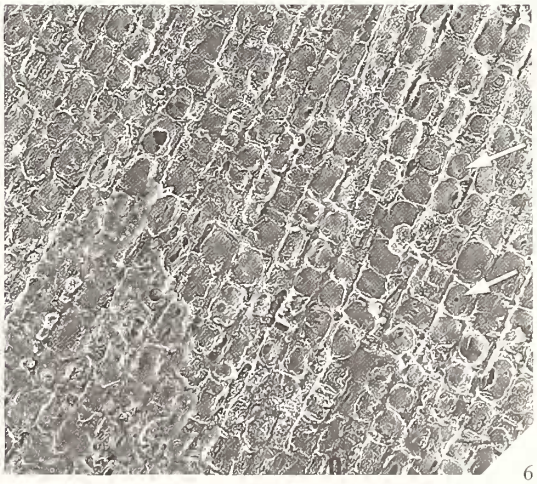
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but the diagnostic criteria used in this assignment were not stated. *Neogoniolithon* has been described from the Oligocene of Italy (Mastrorilli 1967) but the distinctive hypothallium was not illustrated. Poignant (1977) described a coralline from the Palaeocene of the Paris Basin, France, which he considered to be the earliest record of *Neogoniolithon*. However, the illustrated 'megacytes' or 'cellules géantes', that are diagnostic for *Neogoniolithon*, are very large, have irregular shapes and thick micritized walls, and may be borings into the coralline tissue, and not trichocytes. His detailed micrograph of the perithallial tissue does not indicate cell fusions; we consider this to be an incorrect assignment.

Using microstructural analysis we can utilize the same subfamily-level taxonomy for fossil nongeniculate corallines as is currently being employed for present-day corallines, with the exception of the monogeneric subfamily of small epiphytic plants of the Choreonematoideae (Woelkerling 1987) distinguished on the basis of the occurrence of plugs in uniporate sporangial conceptacles. This subfamily, however, is also apparently characterized by the absence of any interfilamental cell-connection (Woelkerling 1988), a feature that presumably can be used for recognition in fossil material. The other three subfamilies are delimited by the type of cell-connections and the number of pores in tetra/bisporangial conceptacles, which are preserved (see identification key, Table 2).

Epithallial cells

Epithallial cells and initials have rarely been described in fossil material but they are preservable, at least in some cases. They are mineralized (Steneck and Paine 1986) and may be preserved, particularly when surrounded by micrite. In addition, coralline thalli can be overgrown by other crusts or other organisms and Voight (1981) described the surface view of epithallial cells of *Fosliella* preserved by overgrowth ('bioimmuration') of encrusters.

Detailed SEM research has allowed us to recognize epithallial cells in vertical section and to employ their characters in delimiting genera, which are currently indistinguishable in thin section. This appears to be the only way of understanding the taxonomy of genera within the Melobesioideae (e.g. *Lithothamnion*, *Phymatolithon* and *Clathromorphum*). Text-figure 2A–B shows the characteristic flat epithallial cells of *Lithothamnion* in a fossil example from the upper Miocene of NE Spain. Epithallial cells are recognizable in fossil Melobesioideae and therefore modern taxonomy can be applied to corallines which currently are all assigned to *Lithothamnion*.

EXPLANATION OF PLATE 2

Fig. 1. *Spongites albanensis* (Lemoine) comb. nov. BMNH V.60928; noncoaxial hypothallial tissue (below) and perithallial tissue above in thin section; note the irregular grid of perithallial tissue and cell fusions (arrowed); Malta; upper Tortonian, Upper Coralline Limestone Formation, × 125.

Fig. 2. *Lithophyllum* sp. Museo de Paleontología Universidad de Granada, Sample TJ-31; detail of perithallial tissue in longitudinal section, showing continuous filament walls; Almanzora Corridor, Almería, Spain; upper Tortonian, × 150.

Figs 3–4. *Spongites albanensis* (Lemoine) comb. nov. Museo de Paleontología Universidad de Granada, Sample PUR-63; Almanzora Corridor, Almería, Spain; upper Tortonian. 3, perithallial tissue in thin section showing bean-shaped conceptacles, irregular grid or spongy aspect and cell fusions (arrows), × 100. 4, SEM view of polished and etched perithallial tissue showing cell fusions (arrowed); direction of growth towards top left, × 200.

Figs 5–6. *Spongites* sp. 1. Museo de Paleontología Universidad de Granada, Sample PUR-28; Almanzora Corridor, Almería, Spain; upper Tortonian. 5, longitudinal section of hypothallial filaments illustrating noncoaxial arrangement of cell divisions and overlying perithallial tissue with cell fusions, × 150. 6, irregular grid or spongy perithallial tissue and uniporate flask-shaped conceptacles; direction of growth towards top, × 40.

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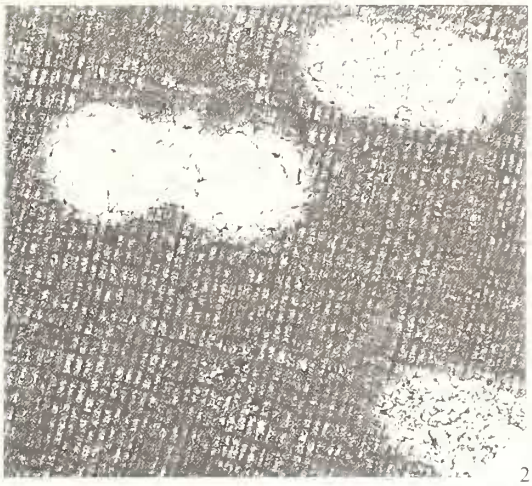

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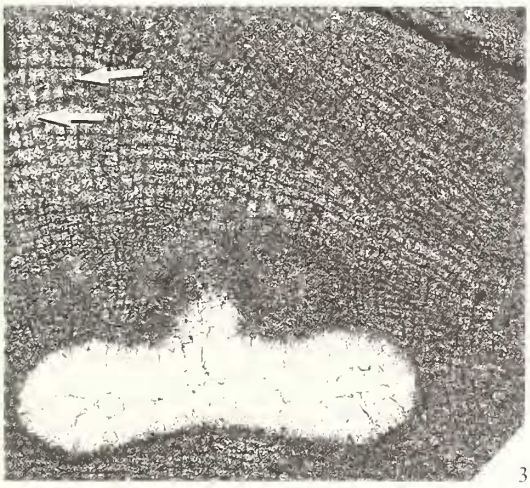

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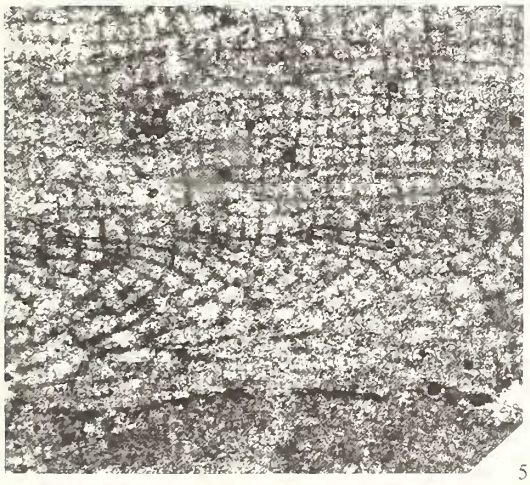

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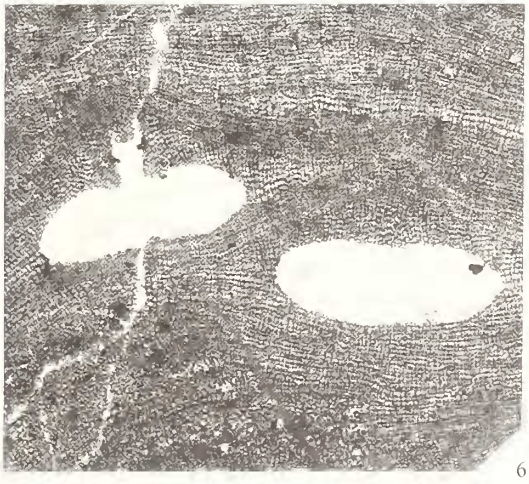

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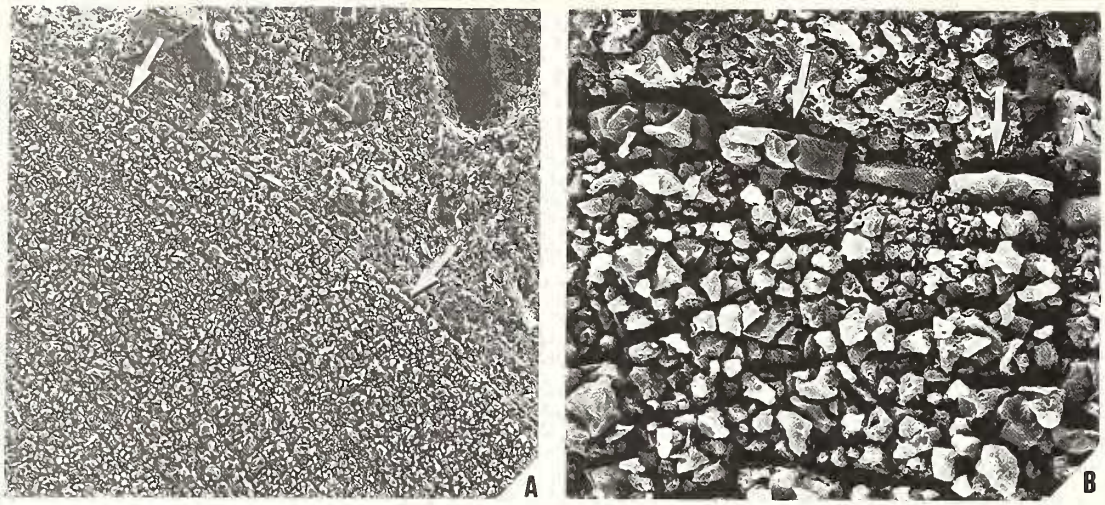

TEXT-FIG. 2. *Lithothamnion* sp. 2. Museo de Paleontología Universidad de Granada, Sample ELX-13; SEM view of epithallial cells (arrowed) in polished and etched section; Elche, Alicante, Spain; upper Tortonian. A, general view of thallus embedded in fine-grained matrix, × 200. B, details of flattened epithallial cells, above rectangular perithallial cells with deeply etched cell walls, × 1000.

IDENTIFICATION KEY

There have been several identification keys published for both present-day (e.g. Adey and MacIntyre 1973) and fossil (e.g. Poignant 1979) coralline algae. The former has the drawback of including characters which are not recognizable in fossils and the latter includes non-diagnostic criteria (e.g. alignment of cells) within the key; both are outdated by the information presented in this paper. A key published by Woelkerling (1988) for the identification of present-day corallines can be followed, but uses many terms which are unfamiliar to palaeontologists. We present a new key (Table 2) for the identification of fossil coralline algae which follows both the revised subfamilial classification presented in Table 1, and the generic classification summarized in Woelkerling (1988) with some additional details from Chamberlain *et al.* (1991) and Penrose and Woelkerling (1992). It includes diagnostic criteria for all non-geniculate corallines which we know have been described from fossil material. For those unfamiliar with coralline algal morphology we recommend that the key should be used alongside Woelkerling's (1988) monograph.

SYSTEMATIC PALAEONTOLOGY

Division RHODOPHYTA Wettstein, 1901
Class RHODOPHYCEAE Rabenhorst, 1863
Order CORALLINALES Silva and Johansen, 1986
Family CORALLINACEAE Lamouroux, 1812
Subfamily MASTOPHOROIDEAE Setchell, 1943
Genus SPONGITES Kützing, 1841

Lectotype species: *Spongites fruticulosa* Kützing, 1841; designated by Woelkerling (1985).

Diagnosis: Nonendophytic Mastophoroideae lacking a basal layer of palisade cells and coaxial hypothallium. Pore canals of tetrasporangial conceptacles bordered by cells that arise from peripheral filaments, protrude into the canals and are subparallel to the conceptacle roof (Penrose

TABLE 2. Key to Cenozoic coralline algal genera using characters preservable in the fossil record. We do not include here (a) the small, epiphytic and taeniform and weakly calcified corallines which are unknown as fossils (Woelkerling 1988) or (b) *Aethesolithon* (Johnson 1964) which has distinctive vegetative tissue but unknown conceptacles. Monomerous – a type of thallus construction involving a single system of repeatedly branched filaments. Dimerous – a type of thallus construction involving two distinct groups of filaments orientated more or less at right angles to one another (Woelkerling 1988).

1. Tetra/bisporangial conceptacles uniporate, cell fusions absent (secondary pits present, but probably not preserved); trichocytes absent (LITHOPHYLLOIDEAE).
   - I. Thallus dorsiventral
     - i. Hypothallium palisade, single layered; margins bistratose (hypothallium and epithallium, if preserved, only) – **Titanoderma** (formerly *Dermatolithon* and most *Tenarea*)
     - ii. Hypothallium mainly non-palisade, single or multistratose, coaxial or non-coaxial; margins multistratose – **Lithophyllum**
   - II. Thallus isobilateral (back to back); crusts with medulla of two layers of palisade cells (unknown as fossil) – **Tenarea**

2. Tetra/bisporangial conceptacles uniporate; cell fusions present (secondary pits absent); trichocytes present or absent (MASTOPHOROIDEAE).
   - 1. Thallus thin, 2–3 (5) cells thick.
     - i. Hypothallium unistratose, small celled; perithallium absent, thin, or only around conceptacles – **Fosliella** (currently indistinguishable from *Pneophyllum* in fossil material).
     - ii. Multiple overgrowths of large (> 10–15 μm diameter) hypothallial cells – **Lithoporella**
   - II. Thallus composed of numerous layers of cells.
     - i. Pore canal of tetrasporangial conceptacles bordered by a ring of elongate and conspicuous cells subperpendicular to the roof surface; cell filaments subperpendicular to the roof surface – **Hydrolithon**
     - ii. Pore canal of tetrasporangial conceptacles bordered by cell filaments subparallel to the roof surface and protruding into the canal
       - a. Hypothallium coaxial; trichocytes absent, single or in vertical or horizontal stacks – **Neogoniolithon**
       - b. Hypothallium non-coaxial; trichocytes absent, single, or in vertical or horizontal stacks – **Spongites**

3. Tetra/bisporangial conceptacles multiporate or sporangial sori; cell fusions present (secondary pits absent) (MELOBESIOIDEAE).
   - I. Tetra/bisporangial conceptacles multiporate.
     - i. Thallus dimerous. Hypothallium unistratose, small celled; perithallium reduced – **Melobesia**
     - ii. Thallus monomerous, composed of numerous layers of cells
       - a. Hypothallium coaxial; epithallium thin and unknown in fossil – **Mesophyllum**
       - b. Hypothallium non-coaxial
         - 1. Epithallial cells flat; epithallium one-cell thick – **Lithothamnion**
         - 2. Epithallial cells not flat
           - a. Epithallium several-cell thick; (unknown as fossil) – **Clathromorphum**
           - b. Perithallial cells show elongation down from meristem; epithallium thin and difficult to recognize in fossils – **Phymatolithon** (currently indistinguishable from *Leptophytum* in fossil material)
   - II. Tetrasporangia in sori; hypothallium non-coaxial. Epithallium thin and unknown in fossil – **Sporolithon** (formerly *Archaeolithothamnium*)

and Woelkerling 1992). In fossil material cell filaments more or less parallel to the conceptacle roof, sometimes protruding into pore canals, can be easily recognized.

Spongites albanensis (Lemoine) comb. nov.

Plate 2, figs 1, 3–4

1924 *Lithophyllum* (?) *albanense* Lemoine, p. 281, text-figs 8–9.
1939 *Lithophyllum* (?) *albanense* Lemoine; Lemoine, p. 105, text-figs 75–77.
1983 *Lithophyllum albanense* Lemoine; Bosence, p. 160, pl. 17, figs 1–4; text-fig. 7.
1988 *Lithophyllum albanense* Lemoine; Braga and Martin, p. 295, fig. 9.

Type specimens. The type material of this species, originated from the Burdigalian of Koritza (Albania), has not been located and seems to be lost. It was illustrated by Lemoine (1924, text-figs 8–9).

Description. Thalli monomerous, forming crusts up to 2 mm thick, which develop into branching protuberances 2–6 mm in diameter and up to 40 mm long. Plumose hypothallium up to 300 μm thick; the cells of which are irregular in size and shape, 15–30 μm (mean 20 μm, S.D. 4) long and 9–15 μm (mean 13 μm, S.D. 2) in diameter (Pl. 2, fig. 1). The perithallial filaments have the aspect of a zoned, spongy grid, both in crusts and in protuberances, where they are radially arranged (Pl. 2, fig. 3). The cells in this part of the thallus are also irregular, 12–20 μm (mean 15 μm, S.D. 2·2) long and 8–13 μm (mean 10 μm S.D. 1·2) in diameter. Fusions between cells of contiguous filaments are common in the perithallium (Pl. 2, figs 1, 3–4) and occasional in the hypothallium.

All the fertile plants bear uniporate conceptacles. They are bean-shaped in section, 400–640 μm (mean 540 μm, S.D. 60) in diameter and 160–220 μm (mean 190 μm, S.D. 25) high (Pl. 2, fig. 3). Pores are surrounded by fans of cell filaments (Pl. 2, fig. 3).

Remarks. This species ascribed to *Lithophyllum* has been reported in the Miocene sediments from many Mediterranean localities. Our material comes from the Miocene of Malta (Bosense 1983) and Almería, Spain (Braga and Martin 1988) and in both cases was assigned to *Lithiophyllum albanense*. The tissue of this species, however, shows clear and abundant cell fusions when observed with the above described SEM method (Pl. 2, fig. 4) and in thin section (Pl. 2, figs 1, 3) and therefore belongs to the subfamily Mastophoroideae and not to the Lithophylloideae. This non-geniculate coralline with cell fusions, a non-coaxial hypothallium and uniporate conceptacles lacking a ring of cell filaments perpendicular to the roof, must be included in *Spongites*.

Spongites sp. 1

Plate 1, figs 1–2; Plate 2, figs 5–6

1988 *Lithophyllum* sp. 1, Braga and Martin, pp. 290, 295, 297.

Description. Thalli of monomerous crusts up to 2 mm thick, that give rise to branching protuberances 2–4 mm in diameter and up to 10 mm in height. Hypothallium multistratose and plumose, 100–200 μm thick (Pl. 2, fig. 5). Hypothallial cells irregularly shaped, 18–32 μm (mean 24 μm, S.D. 3·5) long and 10–18 μm (mean 14 μm, S.D. 1·7) in diameter. Perithallial cells form a slightly zoned, irregular grid with a spongy aspect (Pl. 2, fig. 6) due to cell fusions (Pl. 1, figs 1–2). Cells in this part of the thallus have variable sizes and shapes. Cells are 10–22 μm (mean 16 μm, S.D. 3·5) long and 10–20 μm (mean 14 μm, S.D. 2·2) in diameter. Some isolated cells or vertically arranged groups of cells, which are slightly larger than the average cell-size, may be interpreted with doubt as trichocytes.

Only uniporate conceptacles are present (Pl. 2, fig. 6). They are flask-shaped and are extraordinarily large, measuring 660–1300 μm (mean 980 μm, S.D. 110) in diameter and 200–700 μm (mean 520 μm, S.D. 60) in height from the floor to the roof (not including the pore) of the conceptacle. The conceptacle pore is bordered by fans of cell filaments (Pl. 2, fig. 6).

Remarks. This species would have been ascribed in a traditional palaeontological taxonomy either to *Lithophyllum* or *Neogoniolithon* (see Wray 1977; Poignant 1979) if the larger cells mentioned

above were eventually interpreted as trichocytes. The presence of cell fusions in its tissue, and of uniporate tetra/bisporangial conceptacles, clearly place this alga in the Mastophoroideae. The characters of cells around the pore canal of conceptacles, hypothallium and perithallium are typical of *Spongites* Kützing, 1841 within this subfamily (Woelkerling 1985; Penrose and Woelkerling 1988, 1992).

We prefer not to provide a new name for this alga because of the current revision of the type material of the hundreds of species already established for Cenozoic coralline algae, many of which are poorly described and illustrated. A revision of coralline species taxonomy is beyond the scope of this paper.

CONCLUSIONS

Interfilamental cell-connections can be recognized in fossil corallines using SEM examination of polished and etched sections. The recognition of these anatomical characteristics allows us to employ the same diagnostic criteria in delimiting genera and subfamilies for fossil and present-day corallines. The suprageneric and generic status of some or many Cenozoic species will change after SEM analyses of their tissues. This is exemplified here by *Spongites albanensis* (Lemoine) comb. nov. The recognition of cell fusions in tissues of this coralline permits it to be transferred from the Lithophylloideae to the subfamily Mastophoroideae.

The presence of calcified epithallial cells and initials in some recent corallines suggests the potential preservation of them in fossil material. The recognition of such features in fossil Melobesioideae has allowed us to apply to them the same taxonomic criteria which delimit genera of this subfamily in present-day corallines.

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